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VARIATION IN GROWTH OF YOUNG AND ADULT SIZE IN BARNACLE GEESE *BRANTA LEUCOPSIS*: EVIDENCE FOR DENSITY DEPENDENCE

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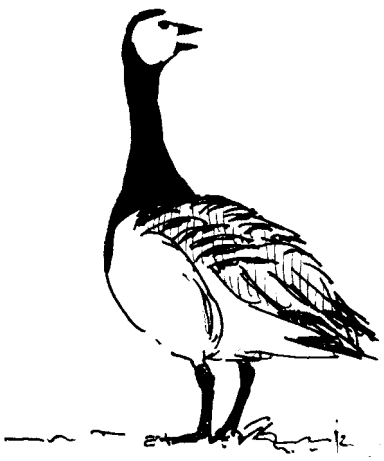

A colony of Svalbard Barnacle Geese *Branta leucopsis* was studied near Ny Ålesund, Spitsbergen. Breeding started in 1980 and the colony size followed a sigmoidal curve with little increase in numbers in the period 1992-1995. Over the period 1991-1995 gosling growth declined, mortality during growth increased and local return rate after fledging decreased. Gosling growth was reflected in final adult body size. Adult geese became smaller over the years. This was more pronounced in ♀♀ than in ♂♂. Individual ♀♀ produced smaller young in later years and also individual adult geese became lighter. All these trends reflect an increasing competition for food over the years. Variation in predation pressure by Arctic Foxes might have amplified the observed trends by reducing the number of goslings (decreasing gosling survival) and restricting the geese to a small feeding area (decreasing gosling growth rate).

Key words: *Branta leucopsis* - Spitsbergen - growth - environmental plasticity - local return rate - survival - philopatry - predation - *Alopex lagopus*

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INTRODUCTION

Most goose populations have increased dramatically in numbers in the last decades (Madsen 1991, Ankney 1996). A change in agriculture (expansion and the use of artificial fertilizer), which provided the geese with high quality food throughout the winter (Owen & Black 1991a) and a reduction of hunting pressure by man (Ebbinge 1985 & 1991) seem the major factors which have led to the observed growth in goose numbers. As a consequence the Arctic breeding grounds had to accommodate more geese, density in individual nesting colonies has increased and the breeding range has expanded (Prestrud *et al.* 1989, Forslund & Larsson 1991, Filchagov & Leonovich 1992, Cooke *et al.* 1995).

Several studies have reported density dependent effects on fecundity and survival in geese (Ebbinge 1985, Cooch *et al.* 1989, Cooch & Cooke 1991, Williams *et al.* 1993, Larsson & Forslund 1994). For Svalbard Barnacle Geese *Branta leucopsis*, there is also evidence for density dependent regulation of population numbers on the breeding grounds. With the increase in numbers, the natural mortality in the period between March and September increased (Owen & Black 1991b) and the recruitment rate declined (Owen & Black 1989 & 1991b).

Growth rate of goslings is highly variable (Cooch *et al.* 1991a, Sedinger & Flint 1991) and dependent on the amount and quality of food plants (Cooch *et al.* 1991b & 1993, Larsson & Forslund 1991, Sedinger *et al.* 1997). A density dependent competition for food should be reflected in growth of goslings. Furthermore, gosling growth rate is reflected in adult body size. Slow growing goslings become relatively smaller adults (Cooch

Table 1. The number of nests counted on various islands in Kongsfjorden. Blanks are years in which no data of a specific area are available. The total is a minimum estimate.

Year	Ny Ålesund	Prins Heinrich	Dietrich-holmen	Miethe-holmen	Stor-holmen	Jutta-holmen	Esk-jaeret	Blom-strand	Total
1980	1								1
1981		0	0	0	0	0	0	0	0
1982		0	0	0	0	0	0	0	0
1983		1	0	3	0	4	0	0	8
1984		0	0	1	0	1	3	0	5
1985		4	0	0	0	7	2	0	13
1986									
1987		19	0	2	7	8	10	0	46
1988									
1989				25					25
1990	10	38	0	5	0				53
1991	22	17	0	3	42	38	17	10	149
1992	7	36			84				127
1993	0	5	5	21	224				255
1994	0	36	10	5	12	0	3	7	13
1995	7	5	4	31	134	61	16	29	287

et al. 1991b, Larsson & Forslund 1991, Sedinger *et al.* 1995). Variation in adult body size can therefore also be used to examine the local conditions on the breeding grounds. In this paper, variation in gosling growth rate, gosling survival and adult body size are used to assess competition for food with increasing density of Barnacle Geese on the breeding grounds.

STUDY AREA AND METHODS

Data were collected near Ny Ålesund (Kongsfjorden) Spitsbergen (78°55'N, 11°56'E). In 1987 and 1989, Barnacle Geese were caught in a cooperation between the Norwegian Polar Institute and the Wildfowl and Wetlands Trust. Birds were ringed with engraved plastic rings with individual combinations of colour and inscription. In 1990, a Dutch team of the University of Groningen started collecting detailed observations on ringed geese during the brood rearing and moulting period and since 1991, this group continued catching and ringing geese. Since the establishment of the colony, the Norwegian Polar Institute has monitored the number of nests (F. Mehlum & I. Tombre unpubl. data). In some years, the survey was not complete, but still covered the major nesting sites (Table 1). Nests were usually counted in the last week of June, one week before hatching. While nesting concentrated on the islands within the fjord, the direct vicinity of the village of Ny Ålesund developed into the main feeding area after hatch. Of all individuals observed nesting in 1993, 90 % was resighted in this area. The largest flock of non and failed breeders in the fjord was also present in this area.

From 1989 to 1995, the number of adults in the population was estimated using a modified Petersen estimate (Begon 1979). All individuals which were ringed in a previous year and sighted at least once during the summer period were regarded as the marked population in a year. The total number of adult geese in the fjord was calculated by dividing the size of the marked population by the proportion of marked adult geese in all catches. For 1989, the marked population size was extrapolated from the number of geese ringed

before 1989 and resighted in each year from 1990 to 1995 in Ny Ålesund. In 1990, the proportion of marked birds was based on observations of flocks, because no geese were caught that year.

Many breeding pairs had at least one ringed parent during our study period. Hatch date of these identifiable families could be established during daily nest checks or by backdating using a gosling age estimate at first sighting for goslings younger than one week (Larsson & Forslund 1991). In 1992, 1993 and 1995 goslings were marked at hatch with a numbered webtag (Alliston 1975). Adoption of goslings (Choudhury *et al.* 1993) could cause a bias in our age estimate of goslings without webtags. Of all goslings webtagged at hatch, 72 individuals were caught later in the season. Nine were found in another family than the family at hatch. Only one of these goslings had moved to a family with a hatch date which differed more than one day. We believe, therefore, that error introduced in the age estimates due to adoption is minor.

In the period up to fledging, several catches were made. All geese caught were individually ringed, sexed, measured and weighed. Weighing of geese started two hours after the beginning of the catch, to allow geese to empty their digestive tract. Body mass was measured with an electronic balance to the nearest 5 g and corrected with 9 g h^{-1} for evaporative loss during the interval between catching and weighing. This mass loss was based on mass losses of goslings and adults between three and four hours after the catch. Body measurements followed Dzubin & Cooch (1992). Total tarsus length was measured in centimetres to the nearest 0.1 mm with dial callipers as the distance between the extreme bending points when the foot was bent at the intertarsal joint and the toes. Mid wing was measured on the outside of the natural folded wing, from the elbow joint to the outside bend of the carpal joint to the nearest 1 mm with a ruler. Head length was measured to the nearest 0.1 mm with dial callipers as the distance between the back of the head to the tip of the bill. Year of birth was exact for birds ringed as goslings. Birds ringed as adult (both with and without goslings) were given a maximum year of birth as the year prior to the year of ringing. These birds could be born earlier but not later. Family relations were established from resightings after ringing.

From 1991-1995, a total of 296 goslings from 121 families with known hatch date were caught. In 1994, no goslings of known age were caught due to an almost complete nesting failure. In the other years, gosling age ranged from 14 to 44 days with an average of 28 days. Body mass, tarsus, mid wing and head length were analysed by constructing hierarchical linear models (Bryk & Raudenbush 1992) with program ML3 (Prosser *et al.* 1991). This method allowed analyses of variances and covariances, while taking into account the nested relationship of several goslings belonging to the same family. The null model showed the average value of the dependent variable in the data set. The unexplained variance was partitioned over the family level (τ^2) and the individual level (σ^2). For each dependent variable, a growth curve was fitted with *age*, age^2, age^3 and *sex* as possible independent variables. Annual variation was tested by entering dummy variables for year in the model. Only when there was a significant contribution of a dummy variable describing a specific year, this dummy variable was entered in the final model. All interactions between explanatory variables were also tested. Significance of the fixed parameters could be derived from the quotient of the parameter estimate divided by its SE, which followed a Z-distribution.

For comparing body size of individuals as gosling and as adult, gosling body size at age 35 days was calculated assuming that the residual of a measurement of a gosling on the calculated growth curve was constant over the time interval between the age at the catch and age 35 days. Prefleding survival of goslings was calculated from brood size observations of ringed parents using a modified Mayfield procedure (Flint *et al.* 1995). We assumed that changes in brood size occurred at the midpoint of the interval between observations. A trend over the years was tested by calculating a weighted regression using all daily sur-

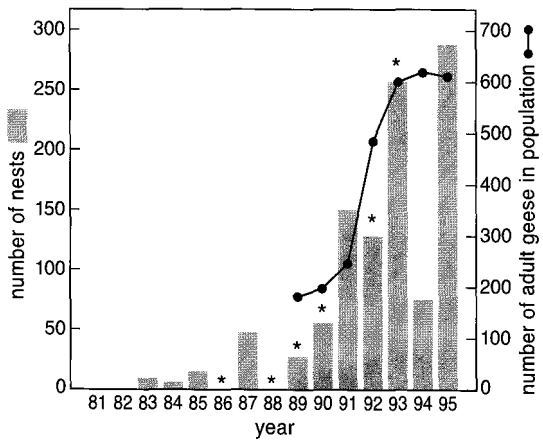

Fig. 1. The number of Barnacle Goose nests in the Kongsfjorden area in different years, together with the calculated number of adult geese in this population. In years marked with an * the nest census was incomplete. For a detailed account see Tables 1 & 2.

vival rates of broods weighted by the number of exposure days for each brood. Annual values were compared using a *Z*-test with a Bonferroni correction of the significance level for multiple comparisons. Local return rate was based on resightings of yearlings, which were ringed as goslings, in our study area.

Adult body size measurements for individuals from different cohorts were calculated as the average of all measurements of an individual in the period 1991-1995. For each year, only the first catch of an individual during moult was used. Body mass change of individual adults in two consecutive years was used to study environmental conditions for adult geese in consecutive years. To minimize the chance for confounding age effects, only adults which were at least two years old were used in this comparison. Body mass differences of individuals between years were tested with a Wilcoxon matched-pairs signed-ranks test. For four breeding pairs of marked geese, it was possible to compare adult body size for offspring from different years. All selected offspring were ♀♀. When there were several individuals per breeding pair in a given year, a gosling was selected at random.

RESULTS

Density of geese

The first breeding record of Barnacle Geese in Kongsfjorden is from 1980, though moulting flocks of Barnacle Geese were seen in 1977 and 1978 (P. Prestrud pers. comm.). Numbers increased exponentially from 46 nests in 1987, 149 nests in 1991 to 283 nests in 1995 (Table 1). There is both variation in the total number of nests over the years and in the number of nests per island, because in some years fast ice enabled Arctic Foxes *Alopex lagopus* to reach the breeding islands during laying. This happened in 1993 on Prins Heinrich and in 1994 on Prins Heinrich

Table 2. Estimation of the number of adult Barnacle Geese in Kongsfjorden on the density of rings in catches and the total number of rings observed. [1]extrapolation, [2]based on sightings.

Year	Caught with ring	Caught without ring	Ring %	Number of rings seen	Estimated population
1989	24	44	35	63[1]	180
1990	221[2]	204[2]	52	102	196
1991	98	152	39	96	245
1992	166	138	55	264	483
1993	174	103	63	377	600
1994	108	63	63	390	618
1995	148	80	65	396	610

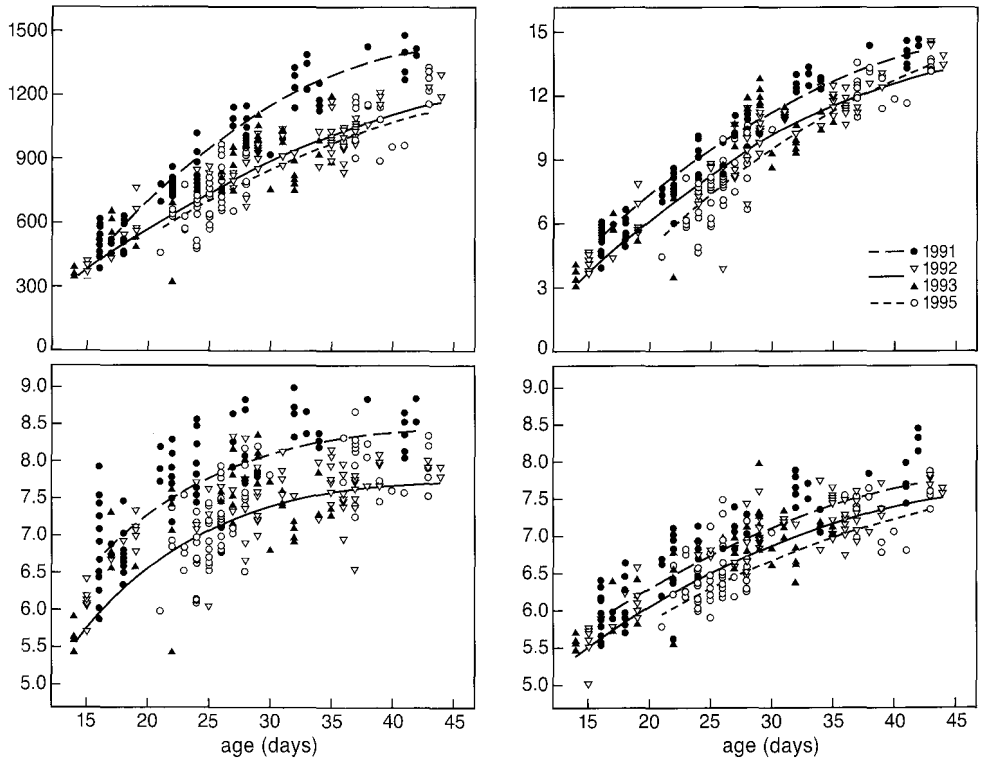

Fig. 2. Growth curves of female goslings for body mass, tarsus, head and mid wing in different years. Hierarchical linear modelling is used to calculate the curves. In 1992 and 1993, the curves did not differ significantly and these years are combined. Tarsus length did not differ in 1995 compared to 1992 and 1993.

and Storholmen. On these occasions, all nests were predated until the fast ice broke up (I. Tombre pers. comm.). The number of adult geese in the Kongsfjorden population is estimated from 1989 onwards (Table 2). In 1989, the local population comprised 180 adults, but from 1991 to 1992 the population doubled from 245 to 483 adults. This was caused by the production of a large number of big goslings in 1991, which survived well and returned as non breeding yearlings in 1992 (see below). Since 1991, the population increased at a slower rate (Fig. 1).

Variation in growth of young

Growth curves for body mass, tarsus length, mid wing and head length are given in Fig. 2. For the null model, the random variance on the family level is much larger than on the individual level (Table 3). Goslings within a family have the same age and hence a similar body size, while different families have various ages. Most parameters used, act mainly on the family level. Only sex is primarily acting on the individual level. As a result the random variance of the final model is more reduced on the family level than on the individual level. The size of a gosling in a specific year can be calculated from the estimates given in Table 3. In 1991, goslings were significantly larger than in other years: at an age of 35 days, goslings were 255 g heavier, and tarsus, mid wing and head were respectively 0.7, 1.0 and 0.2 cm longer in 1991 compared to 1992 and 1993. There was no significant difference in growth between 1992 and 1993 (body mass, $Z = 0.016$, $P > 0.9$; tarsus

Table 3. Results of hierarchical linear models describing growth of goslings with known age in four different years. Only when there is a significant difference for a dummy variable describing a specific year, this dummy variable is entered in the final model.

	null model estimate, SE	Final model estimate, SE	*P*
BODY MASS			
Fixed			
Constant	659.3 (32.7)	-296.5 (80.1)	< 0.001
Age		51.5 (5.1)	< 0.001
Age^2		-0.417 (0.080)	< 0.001
Year 1991		-511.2 (228.9)	0.026
Year 1991 × age		43.3 (17.3)	0.012
Year 1991 × age^2		-0.605 (0.306)	0.048
Year 1995		-35.8 (17.6)	0.042
Sex		42.2 (7.6)	< 0.001
Random			
Variance family level τ^2	135800 (17190)	6031 (950)	
Variance individual level σ^2	13644 (385)	2737 (288)	
Deviance	4205.9	3531.7	
TARSUS			
Fixed			
Constant	7.41 (0.05)	1.13 (0.75)	0.132
Age		0.44 (0.07)	<0.001
Age^2		-0.010 (0.002)	<0.001
Age^3		0.000083 (0.000022)	<0.001
Year 1991		0.73 (0.08)	<0.001
Sex		0.36 (0.04)	<0.001
Random			
Variance family level τ^2	0.310 (0.047)	0.074 (0.014)	
Variance individual level σ^2	0.124 (0.013)	0.074 (0.008)	
Deviance	463.8	217.9	
MID WING			
Fixed			
Constant	9.21 (0.24)	-6.05 (0.75)	<0.001
Age		0.75 (0.05)	<0.001
Age^2		-0.0071 (0.0008)	<0.001
Year 1991		1.13 (0.23)	<0.001
Year 1995		-2.82 (0.71)	<0.001
Year 1995 × age		0.074 (0.024)	0.002
Sex		0.25 (0.07)	<0.001
Random			
Variance family level, τ^2	6.979 (0.907)	0.739 (0.108)	
Variance individual level, σ^2	0.524 (0.055)	0.214 (0.023)	
Deviance	1102.1	666.8	
HEAD			
Fixed			
Constant	6.78 (0.05)	3.43 (0.20)	<0.001
Age		0.16 (0.01)	<0.001
Age^2		-0.0016 (0.0002)	<0.001
Year 1991		0.25 (0.05)	<0.001
Year 1995		-0.15 (0.05)	0.003
Sex		0.25 (0.03)	<0.001
Random			
Variance family level, τ^2	0.276 (0.040)	0.026 (0.006)	
Variance individual level, σ^2	0.071 (0.008)	0.047 (0.005)	
Deviance	341.2	31.5	

Table 4. Pre-fledging survival of goslings as determined from brood size observations of ringed families.

Year	Daily survival rate, ± SE	Number of broods
1990	0.9964 ± 0.0010	41
1991	0.9783 ± 0.0031	65
1992	0.9447 ± 0.0058	81
1993	0.9141 ± 0.0093	114
1994	0.8219 ± 0.0468	13
1995	0.9567 ± 0.0041	160

length, $Z = 0.596$, $P > 0.5$; mid wing length, $Z = 0.302$, $P > 0.7$; head length, $Z = 0.156$, $P > 0.8$). In 1995, goslings were even lighter, with a difference of 43 g compared to 1992 and 1993. For tarsus length, there was no significant variation among 1992, 1993 and 1995, but mid wing and head length were smaller in 1995. Mid wing differed 0.3 cm between 1992-1993 and 1995 and head differed 0.2 cm at age 35. In all models, ♂♂ were larger than ♀♀.

Survival of goslings till fledging

Over the period 1991-1995, daily survival rate of goslings in the period before fledging decreased (Table 4, $F_{1,431} = 5.98$, $P = 0.015$). When goslings had survived the first few days after hatch and arrived on the rearing grounds near Ny Ålesund, the Arctic Fox was the main predator and cause of death (unpubl. data). The annual variation in daily survival rate was reflected in sightings of foxes in the study area. In 1990 and 1991, no foxes were observed during brood rearing. From 1992 to 1994, the number of patrolling foxes observed near the village increased, but was lower again in 1995. The daily survival rate from 1995 was different from 1994 ($Z = 2.87$, $P = 0.002$) and 1993 ($Z = 4.19$, $P < 0.001$) but not 1992 ($Z = 1.69$, $P = 0.047$) using a significance level of 0.016 (Bonferroni correction $\alpha = 0.05/3$).

Local return rate as adult

Local return rate of ringed goslings differed between years ($\chi^2 = 15.08$, $df = 2$, $P < 0.001$). In 1991, 48% of the goslings returned as yearling, compared to 28% and 25% in 1992 and 1993 respectively (Table 5). The difference between years is significant for ♀♀ ($\chi^2 = 27.14$, $df = 2$, $P < 0.001$) but not for ♂♂ ($\chi^2 = 0.8$. $df = 2$, $P > 0.6$), with a nearly significant interaction between sex and year (log-linear analysis, $\chi^2 = 5.91$, $df = 2$, $P = 0.052$). Local return rate of goslings as yearling is female biased. 51% of the ringed female goslings returned the following year, while only 24% of ♂♂ returned. This difference was not caused by differential mortality between the sexes. On the wintering grounds, equal numbers of ringed goslings for both sexes were seen (J. Black unpubl. data). The data from the goslings born in 1989 do not follow the time trend. Only four out of 26 ringed goslings returned to Ny Ålesund in 1990. This return rate was extremely low, while the colony was still relatively small. In 1989, no detailed observations were made on ringed geese in the study area and hatch dates or growth rate of these goslings were unknown.

Table 5. Local return rate of geese ringed as gosling and resighted as yearling in the Kongsfjorden area .

	♂♂			♀♀		
	returned age 1	ringed age 0	%	returned age 1	ringed age 0	%
1991	23	88	26	56	77	73
1992	10	45	22	17	53	32
1993	4	23	17	10	32	31
Total	37	156	24	83	162	51

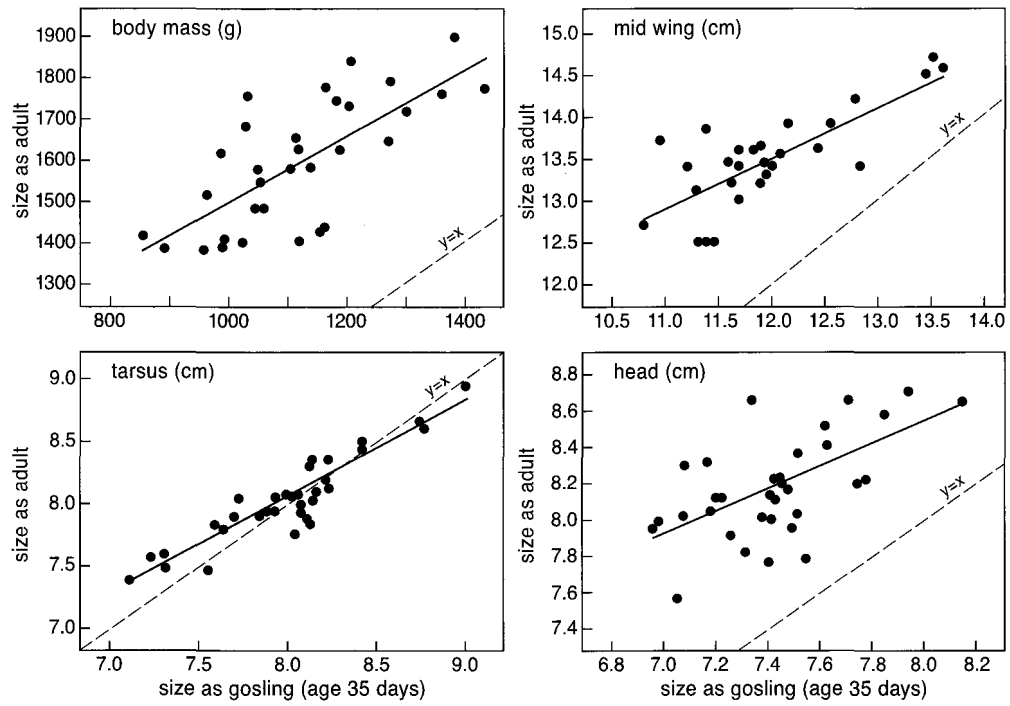

Fig. 3. A comparison between gosling size at day 35 and adult size, as measured during wing moult. The dashed line represents $Y = X$, while the solid line is a linear regression through the data. Large goslings become large adults in later life.

Effect of gosling growth on adult body size

Some goslings returned to the study area as yearling or adult, allowing a comparison of body size as gosling and adult (Fig. 3). For body mass, tarsus, mid wing and head length, there was a significant positive relationship between gosling body size at an age of 35 days and adult body size (Table 6). The slopes of these regressions vary between 0.6 and 0.8 and are less than one because the smallest goslings compensated slightly and increased more in body size from gosling to adult than the largest goslings (Fig. 3). At an age of 35 days, tarsus is almost fully grown and 99% of adult body size. The size at age 35 days for body mass, mid wing and head length is respectively 70%, 89% and 91% of final adult size.

Variation in adult body size among cohorts of known age geese

Since 1990, there was a sharp decline in aver-

Table 6. Linear regression of average adult size against gosling size at age 35 days of individual geese.

	Slope	Intercept	R^2	n	P
Body mass	0.80	695	0.52	33	<0.001
Tarsus	0.77	1.92	0.85	33	<0.001
Mid wing	0.60	6.28	0.59	30	<0.001
Head	0.61	3.66	0.36	33	<0.001

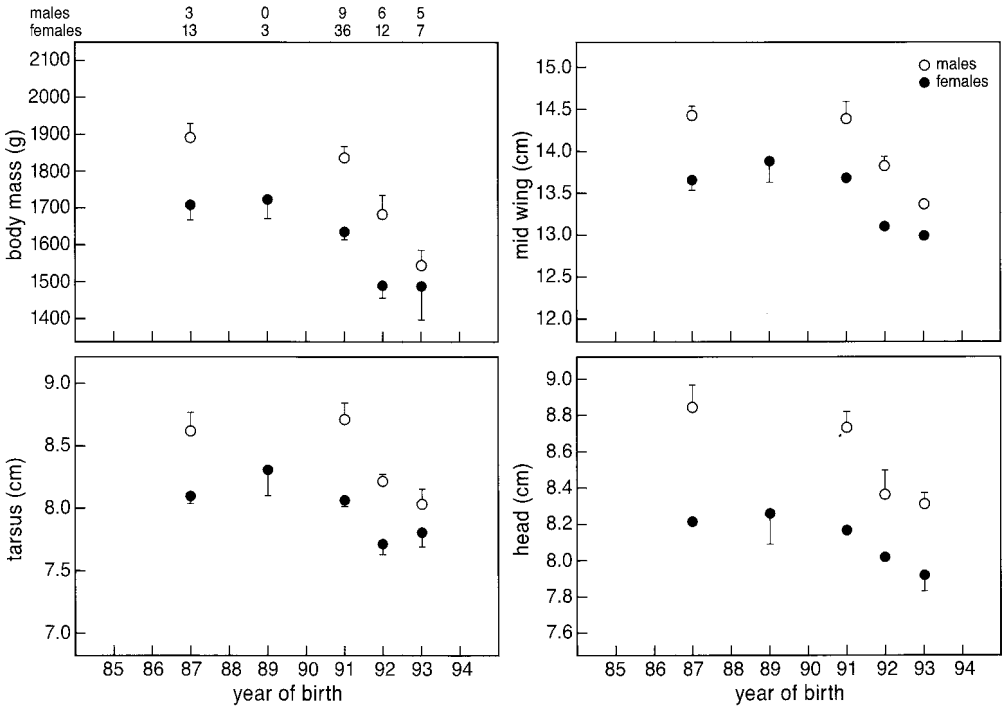

Fig. 4. Body mass, tarsus, head and mid wing of geese born in different years in Kongsfjorden (average with SD). The data are obtained from adult geese caught during wing moult in the period 1991 to 1995 that had been previously ringed as goslings. The numbers refer to the number of individuals in each year.

age mass and tarsus length for adult geese which were born in Kongsfjorden and had been ringed as gosling (Fig. 4). Females born in 1993 were 221 g lighter and had a tarsus 0.3 cm smaller than ♀♀ born in 1987. For ♂♂ these differences were respectively 344 g and 0.6 cm.

Figure 5 shows the same trends for all geese ringed as adults in the study area. Exact ages were not known for these birds. Year of birth could be earlier but not later as the assigned value. The data show a linear declining trend in adult body size with maximum year of birth. Body mass declined 22 g per year ($F_{1,504} = 54.92$, $P < 0.001$), while mid wing declined 0.08 cm per year ($F_{1,486} = 50.72$, $P < 0.01$). In tarsus and head, there was a significant interaction between sex and year of birth (tarsus: $F_{1,504} = 5.85$, $P < 0.05$; head: $F_{1,504} = 4.56$, $P < 0.05$): the declining trends were smaller in ♂♂ than in ♀♀ (tarsus: ♂♂ -0.03 ♀♀ -0.07; head ♂♂ -0.01, ♀♀ -0.04; all in cm per year).

Owen & Ogilvie (1979) reported that in this species body mass increases until two years of age, while other body size measurements stay constant after the first year. The youngest cohorts are measured at a younger age, which could cause confounding effects. Age effects on adult body size were studied using measurements of adults which were born in the period 1991-1993. The average values for mass and total tarsus are given in Table 7. Geese born in 1991 increased in mass from age one to two years. The same was true for geese born in 1993, but geese born in 1992 decreased in body mass from one to two years of age. For this cohort, there was probably an effect of breeding status because in 1994 almost all geese failed before hatch and non breeders are in general lighter than breeding birds (Owen & Ogilvie 1979). In an overall analysis (ANCOVA)

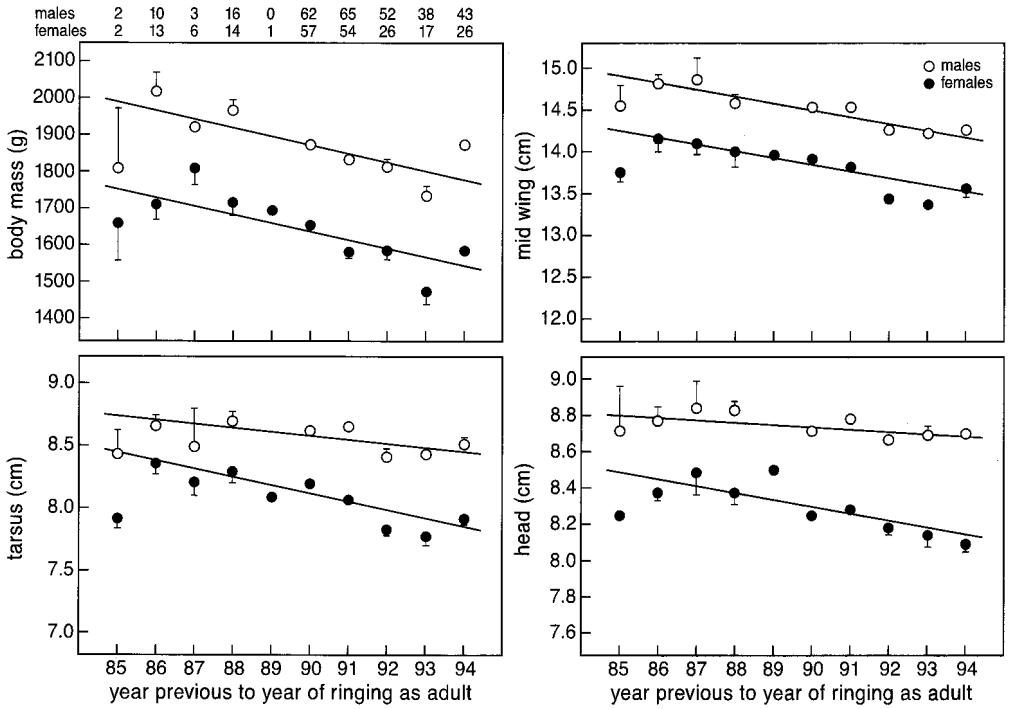

Fig. 5. Body mass, tarsus, head and mid wing of geese ringed as adult in different years in Kongsfjorden (average with SD). The data are collected during wing moult in the period 1991-1995. The maximum year of birth is the year prior to the year of ringing. Numbers refer to the number of individuals of which all measurements in the period 1991-1995 are averaged.

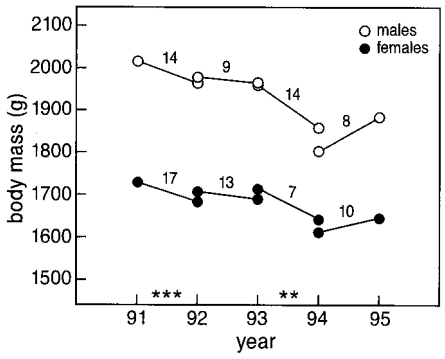

Fig. 6. A direct comparison of body mass during wing moult of the same individual in two consecutive years. The number of individuals used for each comparison between two years is given. There is a significant decline in body mass from 1991-1992 and from 1993-1994.

of body mass using *age* (yearling or older), *sex*, *year of birth*, *year of measurement*, *breeding status* (seen with or without goslings) and *moult stage* (= primary length) all these variables were significant except *age* ($F_{1,94} = 1.61, P = 0.21$). For total tarsus length, there was less variation between years. In an ANCOVA, only *sex* and *year of birth* were significant. *Age* did not contribute significantly to this model ($F_{1,89} = 0.06$, $P = 0.81$) and thus prolonged growth after the first year did not explain the declining trend in adult body size.

Body mass of adult geese varied significantly among years of measurement ($F_{3,95} = 9.38$, $P < 0.001$). In 1994, geese born in 1991 and 1992 were lighter than in 1993 (Table 7). However, different individuals were caught in different years. Therefore, yearly variation in body mass was measured comparing individuals which had been

Table 7. Yearly average values for body mass and tarsus for all adult geese born in a specific year ('-': no data).

Sex	Born	Measured 1992	Measured 1993	Measured 1994	Measured 1995
BODY MASS					
♀	1991	1585	1650	1506	1687
♀	1992		1504	1430	1579
♀	1993			1374	1552
♂	1991	1885	1852	1735	-
♂	1992		1635	1624	1823
♂	1993			1521	1639
TARSUS					
♀	1991	8.0	8.1	8.0	8.0
♀	1992		7.8	7.7	7.6
♀	1993			7.8	7.9
♂	1991	8.9	8.5	8.6	-
♂	1992		8.2	8.2	8.3
♂	1993			8.1	8.2

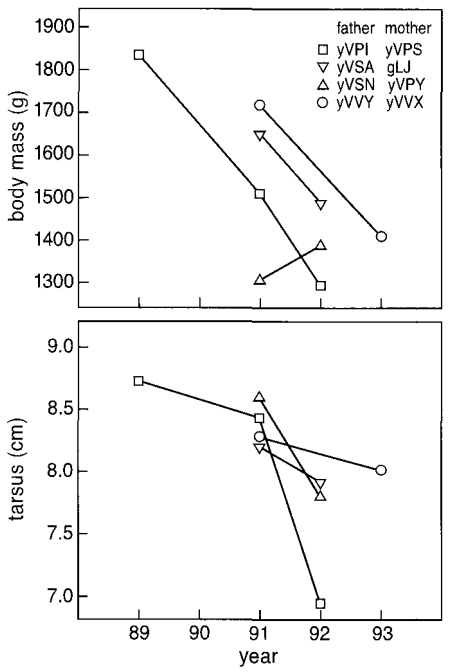

Fig. 7. Birds raised by the same parents in different years show a declining trend in adult body mass and dimensions, which suggests an environmental constraint.

caught in two successive years. To minimize any effect of age in this comparison, only adults that were at least two years old were used in this comparison. From 1991 to 1995, body mass of fully grown individuals declined (Fig. 6). There were significant decreases in mass between 1991 and 1992 (n = 31, Z = -3.40, $P < 0.001$) and between 1993 and 1994 (n = 21, Z = -3.15, P = 0.002). In 1994, body mass was lowest. This year was extraordinary because the geese suffered an almost complete nest failure. Owen & Ogilvie (1979) documented that non-breeders were lighter than breeding birds during the flightless period (time of capture) and the difference between 1993 and 1994 could be explained by a change in breeding status. After selection for adult geese with fledged goslings, there was still a significant decline in mass between 1991 and 1992 (n = 21, Z = -3.15, P = 0.002) and 1991 and 1993 (n = 12, Z = -2.90, P = 0.004). Individual geese which were at least two years old showed a decline in body mass over the study period. Geese raised by the same parents in different years also showed a decrease in adult body size over the years (Fig. 7). For tarsus all direct comparisons declined in size in later

years. For body mass, there was only one comparison where the offspring from a later year was heavier.

DISCUSSION

Since the rapid expansion of the Svalbard Barnacle Goose population in the seventies, both the number of colonies and the density of geese per colony have increased (Prestrud *et al.* 1989). The colony in Kongsfjorden is a good example of these trends. It was established in 1980 and within 15 years, it reached a relatively stable size following a sigmoidal growth curve. After the steep increase in numbers from 1991 to 1992, the population size increased much slower. Is there evidence for density dependence in the study colony?

Gosling growth

Gosling growth is directly affected by food availability and quality (Cooch *et al.* 1991b & 1993, Larsson & Forslund 1991, Lindholm *et al.* 1994, Gadallah & Jefferies 1995) and the declining trend in our data could reflect increased competition for food on the breeding grounds. In 1991 goslings grew much faster than in later years. There was no difference in growth between 1992 and 1993 but in 1995 growth was again slower in three out of four body size variables. Egg size (Sedinger & Flint 1991, Cooch *et al.* 1991a) and weather during the rearing period (Cooch *et al.* 1991b, Lindholm *et al.* 1994) have small but significant effects on gosling growth. Egg size was not measured but might have declined as egg size in Barnacle Geese is correlated with body size (Larsson & Forslund 1992). However, it is unlikely that a decline in egg size is the only factor causing the decline in growth. The effect of cold weather on gosling growth can be direct via increased costs for thermoregulation or indirect via reduced plant growth. There is no trend in temperature and precipitation in July and August over the period 1990-1995 so it is unlikely that this caused the observed decline in gosling growth.

Adult size

Gosling growth is reflected in adult body size (Cooch *et al.* 1991b, Larsson & Forslund 1991, Sedinger *et al.* 1995, this study). This is not surprising for a measurement like tarsus length, which approaches a plateau value in size already before fledging (Fig. 2B). There is very little growth in the tarsus after fledging (Fig. 3B). Body mass and the length of mid wing and head during adult life also reflect growth conditions as a gosling though these measures continue to increase after fledging. For all four body size variables, adults born in 1992 and 1993 are smaller than those born before that year. Geese ringed as adult showed a linear decline in body size against time, differing in magnitude between the sexes (Fig. 5). The most direct evidence for an effect linked to local conditions in our specific area is to consider the female adults, as on account of their strong philopatry the majority will have originated in Kongsfjorden. When growth conditions for goslings deteriorate, there can also be an effect on adult body condition. We therefore compared body mass of adult geese over two consecutive years and found again that these declined (Fig. 6). Such a change in an individual supports the hypothesis that the observed decline in body size is environmentally induced.

Survival

Survival of goslings to fledging can also be a measure of increased competition for food. Such an effect has been found in the Lesser Snow Goose *Anser caerulescens caerulescens* (Williams *et al.* 1993) and Barnacle Goose in the Baltic (Larsson & Forslund 1994). In our study, survival till fledging also decreased. This survival is strongly correlated with the presence of Arctic Foxes in our area and is, therefore, not an unbiased density dependent index as in studies by Larsson & Forslund (1994) and Williams *et al.* (1993). The slowdown in population increase since 1992 could, at least partially, be attributed to the increased predation pressure on goslings. However the observed decline in growth of goslings, local return rate and adult size showed that competition for food also increased.

While the Svalbard Barnacle Goose population increased from 7200 in 1977 to 12 100 in 1989, average survival of ringed goslings decreased from 80% to 62% (Owen & Black 1991a). We observed a similar trend in local return rate in our (relatively young) colony over the period 1991-1993. The small increase in population size since 1991 was not only caused by few goslings surviving to fledging, but also fewer goslings returned as yearling to the natal colony. The decline in growth rate of goslings can be an explanation for the observed reduction in local return rate, congruently with the correlation which was shown by Prop *et al.* (1984), between a summer feeding parameter (feeding time per step) and the survival of the same individual goslings during autumn migration. Owen & Black (1989) showed independently that the heaviest goslings have the best chance for survival during autumn migration in a specific year. In our data, we compare different years but show a similar trend. We have not used survival, but local return rate as yearling to the breeding grounds and found a significant difference between the sexes. This difference is not caused by differential mortality between the sexes, because the resighting rate of these geese in their second winter is equal for both sexes (J.M. Black unpubl. data). There seems to be a female-biased philopatry, which was already well known for many waterfowl species (Cooke *et al.* 1975, Rohwer & Anderson 1988), but which was not documented for the Barnacle Goose. Interestingly, Owen *et al.* (1988) found that geese tend to pair with mates with which they have been moulting in their first year, while Choudhury & Black (1994) experimentally confirmed this. However both studies were based on the association of geese as yearlings and this study shows that ♂♂ have already dispersed from their natal colony at that age. The critical step is thus from the first wintering site to a prospective moulting site in the second year of life, and it would be worth investigating what factors influence this decision.

Density dependence?

Competition for food is generally regarded as the major factor limiting bird numbers (Martin 1987). The amount of food per capita is difficult to quantify. When competition for food increased, Lesser Snow Geese started to use alternative feeding areas (Cooch *et al.* 1993) and plants of lower quality which had a negative effect on gosling growth (Gadallah & Jefferies 1995). In our study area, the most important grazing area was heavily used in all years of study and most variation between years occurred in the use of alternative areas. The presence of Arctic Foxes since 1992 restricted families to the vicinity of open water to escape from predation. In this manner, competition for food increased more than would be expected on the basis of the goose numbers alone, despite the reduction in the number of goslings by predation. A comparison of trends in adult size over different colonies revealed that the decline in adult body size in the Kongsfjorden colony is the steepest decline recorded in the Svalbard Barnacle Goose (J.M. Black unpubl. data). Prop *et al.* (1984) calculated a maximum density of ten Barnacle Geese per hectare moss on Nordenskiøldkysten during the flightless period. The total area wet moss near Ny Ålesund was about six ha, while there were usually more than 100 geese feeding in this area. The density of geese per area wet moss in Ny Ålesund exceeded the maximum density as recorded for Nordenskiøldkysten

There are two alternative explanations for the decline in growth rate over the years other than food availability alone. First, a selection pressure might have changed the genetic structure of the colony towards smaller birds. Apart from a substantial environmental variation in avian adult body size, primarily due to variation in food availability during juvenile growth, there is also a heritable component in adult body size variation (Larsson 1993). However, effects of a different genetic structure are excluded when the same individuals are compared in several years. Full grown adult geese became lighter from one year to the next (Fig. 6) and offspring raised by the same parents in different years also became smaller (Fig. 7), so this possibility can be rejected.

Second, parasites can be responsible for a density dependent regulation of bird numbers (e.g. Hudson & Dobson 1991). A density dependent effect on growth could be caused by a parasitic infection which has an effect on growth rate of goslings as has been found in Cliff Swallows *Hirundo pyrrhonota* (Chapman & George 1991). When density of birds increases, the chance of parasitic infection can also increase. If infection with parasites would reduce growth, a relation with density would result. At present, we cannot rule out this possibility, but a pilot experiment in 1995 showed only marginal effects of intestinal parasites on growth and absence of haematozoan infections (A. Boele unpubl. data).

The observed trends in growth rate, body size and survival all suggest an increase in competition for food and a density dependent regulation of goose numbers in our study area. The increasing presence of Arctic Foxes might have reinforced the observed trends by restricting foraging opportunities.

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SAMENVATTING

Het aantal Brandganzen in een kolonie rond Ny Ålesund (Kongsfjorden, Spitsbergen) is sinds 1980 toegenomen volgens een sigmoïde curve: na een aarzelend begin volgde een periode van snelle groei (1991-1992), waarna de populatie zich min of meer stabiliseerde

(Fig. 1). Een dergelijke toename suggereert het bestaan van een dichtheidsafhankelijke regulatie van de populatiegrootte. De groei en overleving van ganzenkuikens is nader onderzocht om dit te onderbouwen. Over de periode 1991-1995 nam de groei van de kuikens af, terwijl de sterfte van deze kuikens toenam en keerden minder vliegvlugge kuikens als adult terug naar het studiegebied. De groeisnelheid van een kuiken werd weerspiegeld in de uiteindelijke grootte als adult. Zo bleken ganzen die waren geringd in de periode dat de populatie nauwelijks toenam in aantal, kleiner dan ganzen die werden geringd ten tijde van de snelle groei van de broedpopulatie. Deze trend is duidelijker bij ♀♀ dan bij ♂♂ omdat de meeste ♀♀ zijn geboren in het studiegebied, terwijl een deel van de ♂♂ van elders kwam. Volwassen adulte ganzen zijn lichter in een volgend jaar en hetzelfde ganzenpaar produceert in een later jaar kleinere nakomelingen, dan de nakomelingen die in een eerder jaar geboren zijn. De waargenomen trends in kuikengroei, lichaamsgrootte en overleving duiden op een toegenomen concurrentie voor voedsel in het studiegebied en dus op dichtheidsafhankelijke regulatie van de aantallen ganzen. De toegenomen predatiedruk door poolvossen kan de waargenomen trends hebben versterkt, doordat kuikens worden gepredeerd (afgenomen overleving) en doordat de ganzen zich moesten concentreren in de veiligste voedselgebieden (beperking foerageergebied, afgenomen kuikengroei).

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